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MICROHABITAT SELECTION BY THE JOHNNY DARTER, *ETHEOSTOMA NIGRUM* RAFINESQUE, IN A WYOMING STREAM

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ABSTRACT.—Microhabitat selection by the johnny darter (*Etheostoma nigrum*) was examined in the North Laramie River, Platte County, Wyoming, where it does not occur with other darter species in the same stream reach. Electivity indices based on microhabitat observations indicate that *E. nigrum* avoids riffles and selects certain microhabitats characterized by intermediate water depths in pools and slow-moving runs with a substrate composed primarily of silt and sand. Niche breadth and electivity values for total depth, bottom water velocity, and substrate measurements from this study indicate that *E. nigrum* is a habitat generalist, except at the extreme ends of the habitat gradient. Habitat use here is generally similar to other studies where *E. nigrum* occurred with one or more other darter species. This study found little evidence for competitive release in the absence of other darters.

Key words. microhabitat use, Percidae, niche breadth, competitive release, electivities, morphological specializations, Etheostoma nigrum.

The johnny darter exhibits the largest geographic distribution among the North American darters (Etheostomatini: Percidae), with the possible exception of *Percina caprodes*. It occurs farther west than any other darter except *Etheostoma exile* (Page 1983). The ecology of *E. nigrum* has received considerable study, often in conjunction with other darter species (e.g., Winn 1958, Smart and Gee 1979, Paine et al. 1982, Englert and Seghers 1983, Mundahl and Ingersoll 1983, Martin 1984). The ability of *E. nigrum* to colonize such a large geographic area may be explained in part by its tolerance of a variety of environmental conditions (Scott and Crossman 1973, Trautman 1981, Becker 1983).

Throughout most of its range, *E. nigrum* coexists with one or more darter species in streams (McCormick and Aspinwall 1983, Schlosser and Toth 1984, Todd and Stewart 1985). *E. nigrum* is also commonly found in lakes with weedy or sandy shorelines (Page 1983). Coexisting darters typically show resource partitioning along food and habitat axes (Smart and Gee 1979, Paine et al. 1982, Matthews et al. 1982, White and Aspinwall 1984, Todd and Stewart 1985). In addition to *E. nigrum*, the Iowa darter (*E. exile*) and the orangethroat darter (*Etheostoma spectibile*) occur in the upper Platte River drainage of eastern Wyoming. Both *E. nigrum* and *E. exile* occur in a tributary of the North Platte River, the Laramie River, and several of its tributary streams, but have not been recorded as co-occurring there (Baxter and Simon 1970, Page 1983).

The purpose of this paper is to examine the microhabitat use of *E. nigrum* at the western extreme of its range where it does not coexist with other darter species in the same reach of stream. Two basic questions are addressed: (1) Are the microhabitat requirements significantly different for *E. nigrum* in the study stream compared to other streams in North America where it is found? (2) Does *E. nigrum* show signs of competitive release in the absence of other darters?

STUDY AREA

The North Laramie River, Platte County, Wyoming, drains the central Medicine Bow Mountains and is a tributary of the Laramie River, which in turn joins the North Platte River near the town of Wheatland. The study was confined to a 100-m reach of river approximately 10 km upstream from Interstate Highway 25 (elevation 1426 m). At this location the river traverses a broad floodplain averaging 0.75–1.0 km in width. Dominant overstory riparian vegetation includes cottonwood (*Populus deltoides*) and various tree and shrub willows (*Salix* spp.). The study area is

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sparsely populated with large cattle ranches and alfalfa farms bordering the lower to middle reaches. The most noticeable result of these land-use practices has been removal of riparian vegetation and consequent associated sedimentation; however, fencing has effectively excluded cattle from the North Laramie River along the study reach.

The study reach, chosen as representative of the lower portions of the North Laramie River, is generally characterized by large, relatively uniform, shallow pools connected by short riffles and runs of varying water velocities. Wetted stream channel width within the study reach averages 6.5 m with a gradient of 4.7 m/km. This contrasts with gradients within the middle reaches of the North Laramie River of 15.1 m/km. Stream discharge at the study site averages 0.17 m^3/s, although short-term fluctuations in flow may occur from summer thunderstorms and irrigation diversions. The substrate ranges from a dominance of small gravel and sand, silt, and detritus in pools to medium to large gravel and cobble in riffles and runs. Diel water temperatures in summer typically range from 13.5 to 21 C. Minimum underwater visibility in the river was 2.5 m or greater during the study. Rooted aquatic vegetation within the study reach includes waterweed (*Elodea canadensis*), perfoliate pennycress (*Thlaspi perfoliatum*), and *Ranunculus longirostris*.

METHODS

Microhabitat observations of *E. nigrum* were made 7–12 September 1988. Undisturbed fish were located by a single observer snorkeling in an upstream direction. Because of the high water clarity, relatively close spacing of individual fish, and their observed habit of remaining in direct contact with the substrate, marking the location of fish was not a problem. Typically the locations of 4–7 individuals were noted and marked by placing a white golf ball on the substrate. This approach allowed the snorkler to maximize the number of undisturbed individual observations and minimize disturbance to upstream fish.

For each individual observation the following microhabitat data were recorded: (1) total depth of the water column, (2) focal point elevation (vertical distance of the fish from the bottom), (3) focal point velocity (water velocity at the fish's snout), (4) mean water column velocity, (5) surface velocity, (6) substrate composition, and (7) cover type. Velocity measurements were made with a mini flow meter (Scientific Instruments, Inc., Model 1205). Mean water column velocity was measured as the velocity at 0.6 of the total depth when the total depth was less than 0.75 m, or the mean velocities at 0.2 and 0.8 of the total depth when greater than 0.75 m (Bovee and Milhouse 1978). Relative depth, a measurement of the location of the fish in the water column, was calculated by subtracting focal-point elevation from total depth and dividing by total depth. All observed individuals were greater than 25 mm standard length; however, no effort was made to distinguish between juvenile and adult fish.

Nine codes were used to characterize substrate composition (percentage) in an area 0.15 m on a side measured from beneath each fish: 1, fines (sand and smaller); 2, small gravel (4–25 mm); 3, medium gravel (>25–50 mm); 4, large gravel (>50–75 mm); 5, small cobble (>75–150 mm); 6, medium cobble (>150–225 mm); 7, large cobble (>225–300 mm); 8, small boulder (>300–900 mm); and 9, large boulder/bedrock (>900 mm). A cover rating (0–2) as measured by the relative degree of protection of fish from stream velocity, visual isolation, and light reduction (i.e., shading) was assigned to each observation. A rating of 0 denoted no protection; 1, moderate protection; and 2, major protection. The general type and location of cover in relation to fish also were noted.

Habitat availability was determined randomly each day immediately following the collection of microhabitat-use data (Moyle and Baltz 1985). The following availability measurements were made along 10 randomly selected transects within the study reach: total depth; bottom, mean water column, and surface velocities; substrate composition; and cover type. Between 15 and 30 equally spaced measurements were made along each transect. To adequately characterize habitat availability within the comparatively short study reach, an effort was made to collect approximately twice as many measurements of habitat availability as microhabitat observations.

An electivity index was used to determine selectivity by *E. nigrum* for total depth, bottom water velocity, and substrate composition. Electivities were calculated from the formula $D = r - p/(r + p) - 2rp$, where r is the proportion of the resource used and p is the proportion available

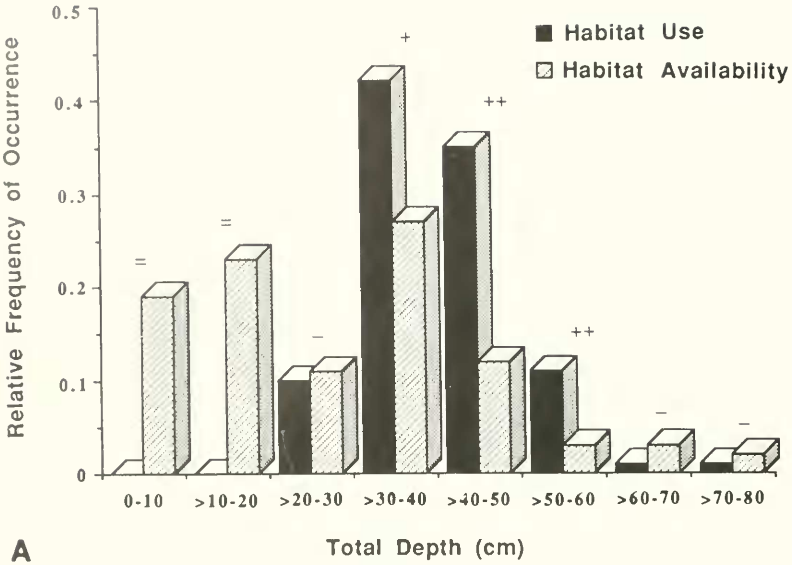

Fig. 1A. Relative frequency distributions of microhabitat use and availability for total water column depths for *E. nigrum* in the North Laramie River. Electivities are indicated ++ (>0.50, strong preference), + (>0.25 but <0.50, moderate preference), 0 (±0.25, no preference), − (>−0.05 but <−0.25, moderate avoidance), and = (<−0.05, strong avoidance).

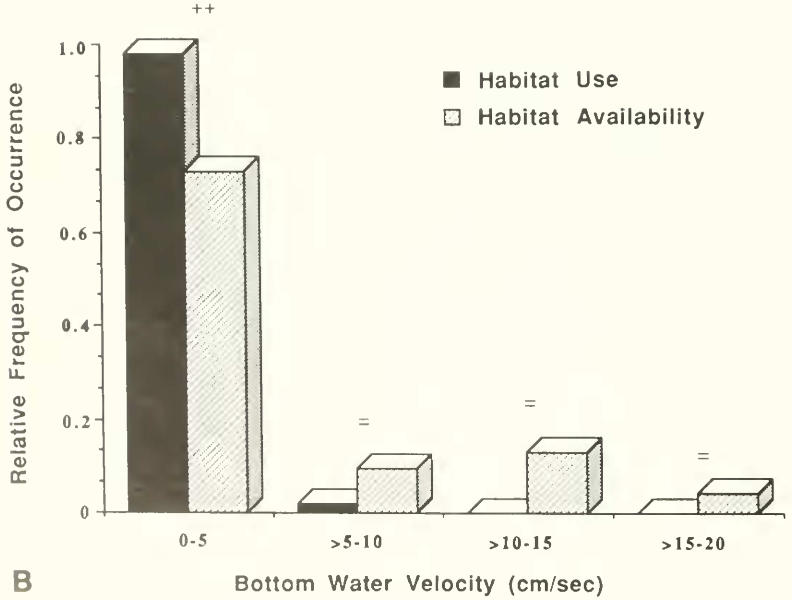

Fig. 1B. Relative frequency distributions of microhabitat use and availability for bottom water velocities for *E. nigrum* in the North Laramie River. Electivities are indicated ++ (>0.50, strong preference), + (>0.25 but <0.50, moderate preference), 0 (±0.25, no preference), − (>−0.05 but <−0.25, moderate avoidance), and = (<−0.05, strong avoidance).

in the stream environment. This index is based on the formula by Jacobs (1974), as modified by Moyle and Baltz (1985) for determining microhabitat selectivity from variables similar to those used in this study. A Kolmogorov-Smirnov test for goodness of fit was applied to frequency distributions for habitat use and availability to determine whether maximum differences between the observed and expected distributions were significant (Sokal and Rohlf 1981).

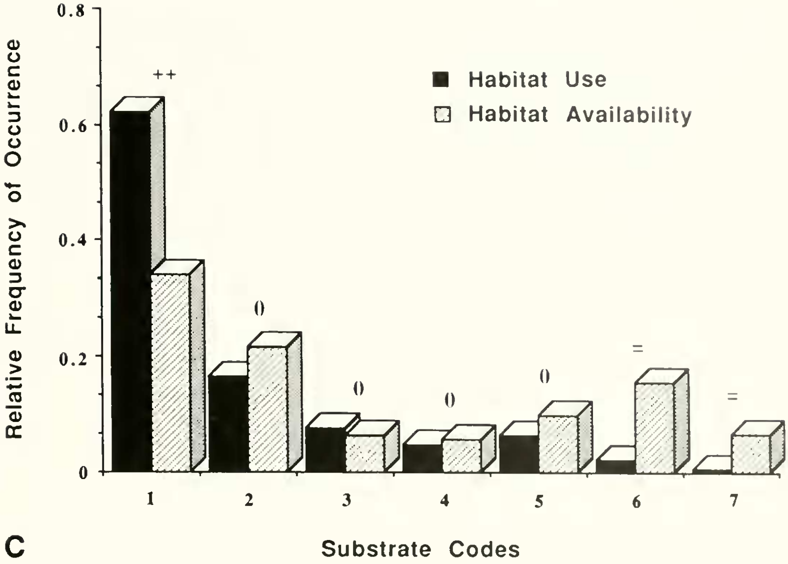

Fig. 1C. Relative frequency distributions of microhabitat use and availability for substrate codes for *E. nigrum* in the North Laramie River. Electivities are indicated ++ (>0.50, strong preference), + (>0.25 but <0.50, moderate preference), 0 (+0.25, no preference), − (>−0.05 but <−0.25, moderate avoidance), and = (<−0.05, strong avoidance).

An additional measure of microhabitat utilization, niche breadth, was calculated for E. nigrum. Two measures of niche breadth were calculated to adequately characterize the effect that the selectivity of rare and common resources might have on niche-breadth values. Hurlbert's measure of niche breadth (B′), which is sensitive to the selection of rare resources, was calculated as follows: $B'=1/\Sigma(p_j^{2}j/a_j)$. Smith's measure of niche breadth (*FT*), which is less sensitive to the selectivity of rare resources, was calculated as follows:

$$FT = \sum_{j=1}^{n}(\sqrt{p_j a_j})$$

where p_j equals the proportion of individuals found in resource $j(\Sigma p_j = 1.0)$, and a_j is the proportion of total available resources consisting of resource $j(\Sigma a_j = 1.0)$ (Krebs 1989). B' values were standardized to a scale of 0–1, using the equation $B'_A = B' - a_{min}/1 - a_{min}$, where B' equals Hulbert's niche breadth, and a_{min} equals the smallest observed proportion of all resources (minimum a_j). The larger the B' and *FT* values, the less individuals discriminate between resource states (minimum specialization); the smaller the B' and *FT* values, the greater the resource discrimination (maximum specialization).

RESULTS

Eight species of fish were observed with E. nigrum at the study site. These were sand shiner (*Hybognathus hankinsoni*), suckermouth minnow (*Phenacobius mirabilis*), creek chub (*Semotilus atromoculatus*), common shiner (*Notropis cornutus*), red shiner (*N. lutrensis*), bigmouth shiner (*N. dorsalis*), white sucker (*Catostomus commersoni*), and rainbow trout (*Oncorhynchus mykiss*).

Microhabitat Observations and Habitat Availability

Microhabitat-use data indicated that *E. nigrum* always occurred in continuous contact with the substrate where water velocities were low (Table 1). *Etheostoma nigrum* was almost exclusively found over a substrate of sand or small gravel, usually in pools and slow-moving runs of intermediate depth (Table 1, Figs. 1A–C). In contrast, surface velocities often were relatively high.

In this study, observations indicated that individual fish were positioned (1) on the surface of the exposed substrate with no apparent cover, (2) immediately below the front edge of a slight depression in the sand that served to protect fish from the current, or (3) rarely on the downstream slope of a small cobble also protected from the current. In all cases, *E. nigrum*

TABLE 1. Means (± S.D.) from microhabitat use and availability measurements for *E. nigrum* in the North Laramie River, Wyoming.

Variable	Habitat use observations	Habitat availability
Total depth (cm)	40.5 ± 8.8	27.1 ± 16.8
Focal point evaluation (cm)	0.1 ± 0.01	—
Relative depth (cm)	0.9 ± 0.02	—
Mean water column velocity (cm/s)	2.6 ± 4.5	3.7 ± 6.4
Focal point/bottom velocity (cm/s)	0.2 ± 0.7	1.8 ± 3.1
Surface velocity (cm/s)	5.2 ± 7.3	5.4 ± 8.2
Substrate types (%)		
(1) fines	62.1 ± 35.8	34.1 ± 36.3
(2) small gravel	16.5 ± 19.6	21.6 ± 25.6
(3) medium gravel	7.6 ± 14.7	6.4 ± 13.3
(4) large gravel	4.7 ± 13.5	5.8 ± 14.9
(5) small cobble	6.3 ± 15.7	9.7 ± 21.5
(6) medium cobble	2.1 ± 11.3	15.5 ± 28.7
(7) large cobble	0.7 ± 0.20	6.5 ± 21.5
(8) small boulder	—	—
(9) large boulder	—	—
Cover code[1] (0–2)		
Stream velocity	1.5 ± 0.6	—
Visual isolation	0.5 ± 0.6	—
Light reduction	0.1 ± 0.3	—
Sample size	91	168

[1] Refer to Methods.

TABLE 2. Niche breadth values (B'_A and *FT*) for *E. nigrum* for total depth, bottom water velocity, and substrate in the North Laramie River, Wyoming (approximate 95% confidence interval shown in parentheses).

	Total depth	Bottom velocity	Substrate
Hurlbert's B'_A	.45 (.41, .49)	.76 (.72, .80)	.70 (.66, .74)
Smith's *FT*	.72 (.65, .78)	.89 (.84, .93)	.93 (.89, .96)

positioned itself in close proximity with other types of instream cover (e.g., stones, cobbles, branches, or small depressions in the sand). The average distance to such cover was less than 6 cm for 89% of the observations.

Measurements of microhabitat availability indicated that average water depths available to *E. nigrum* were shallower than the depths at which it was typically observed (Kolmogorov-Smirnov test, .23, $p < .01$), and available mean bottom water velocities were greater than where fish were observed (K-S test, .25, $p < .01$; Figs. 1A, B). In addition, available substrate was dominated by fines and small gravel (55%), but this was disproportionately low when compared with microhabitat use observations for these same substrate types (79%; K-S test, .28, $p < .01$; Fig. 1C).

Habitat Selection and Niche Breadth

Electivity indices indicate that E. nigrum was selecting certain microhabitats while avoiding others. E. nigrum selected intermediate water depths and avoided high mean water column velocities (Figs. 1A, B). There was a strong selectivity for a substrate composed of sand, and an avoidance of medium to large cobbles (Fig. 1C). Fish generally avoided areas that (1) exhibited high surface water velocities, (2) were isolated visually, or (3) were well shaded by physical cover (Table 1). Rather, fish utilized relatively barren substrates exposed to full sunlight but close to cover. Microhabitat niche breadths (B'_A and *FT* values) for depth, velocity, and substrate indicate little resource specialization by E. nigrum (Table 2).

DISCUSSION

The results of the electivity indices and the K-S test indicate that *E. nigrum* is highly selective in the microhabitats it occupies. However, niche breadth values suggest that *E. nigrum* does not discriminate between available microhabitats (i.e., minimal habitat specialization). The apparent inconsistency between niche-breadth values and electivity indices may be explained by two factors: (1) the relative scarcity in the study area of gravel/cobble riffle habitats and their avoidance by darters, and (2) the preference by darters for low-velocity pool habitats characterized by sand and small gravel, a habitat that was abundant in the study area. Values for Hurlbert's measure of niche breadth (B'_A) were consistently lower than values for Smith's measure (*FT*) for depth, velocity, and substrate. This is expected because B'_A is sensitive to the selection of rare resources that are more heavily weighted in the calculation of niche breadth, while *FT* is less sensitive to the selection of rare resources (Krebs 1989).

Darter species typically are restricted to a narrow range of microhabitats. This is especially evident in their use of certain substrates (Page 1983). *E. nigrum* has an unusually broad tolerance among darters for variable environmental conditions and has been observed over widely varying velocities, depths, and substrates between drainages and within a particular stream reach (Smart and Gee 1979, Angermeier

1987). This study and others (e.g., Becker 1959, Paine et al. 1982, Englert and Seghers 1983) generally show that *E. nigrum* occurs most frequently in pools and sluggish reaches of stream over sand or silt substrates, although this darter also regularly occurs in riffles (Lachner et al. 1950, Smart and Gee 1979, Trautman 1981). In other streams, pool and riffle habitats are often coinhabited by one or more darter species. If competition with other darter species restricts *E. nigrum* to microhabitat types in which they are commonly found, then in the absence of other darter species one might expect *E. nigrum* to experience competitive release. *Etheostoma nigrum* when alone should occupy a wider range of habitat in a particular stream reach, without as much specialization for a particular range or resource type. Observed patterns of microhabitat use from this study found little evidence of competitive release, suggesting that other darters are probably not restricting *E. nigrum* to a particular habitat type in streams where they coexist.

Electivity and niche-breadth values for depth, velocity, and substrate measurements from this study support the conclusion of Coon (1982) and others (Winn 1958, Karr 1963) that *E. nigrum* is a habitat generalist, except at the extreme ends of the habitat gradient (i.e., shallow cobble riffle and very shallow pool habitats). However, in contrast to the studies of Coon (1982) and Smart and Gee (1979), that recorded *E. nigrum* in riffle and run/pool habitats with one or more darter species, in this study *E. nigrum*, while it was common in pools, did not occur in riffles even in the absence of other darters.

Schlosser and Toth (1984) suggested that differences in microhabitat use in two sympatric darters appear to be constrained by morphological specializations of each species rather than by interspecific competition. As with most small darters, *E. nigrum* is characterized by morphological specializations best suited to the benthic stratum of pools and other sluggish stream habitats, often with a sand or silt substrate (Page 1983, Page and Swofford 1984). Support for the role of morphology in driving habitat utilization by *E. nigrum* in the study area comes from data on cover utilization. Protection from stream velocities in the absence of any apparent physical instream cover may be explained by this species' small size and benthic habits. Velocities immediately above the substrate where fish were observed were negligible when compared to velocities at the same location a few centimeters higher in the water column or at the surface. Also, subtle depressions in the sand substrate often were occupied by individual fish presumably for protection from stream velocity. One might expect that the small size and observed patterns of habitat utilization by *E. nigrum* would increase its risks to predation. However, small size, drab coloration, speckling, W-marks, and partial translucence, combined with exposure to full sunlight, made detection of individual fish on the speckled sand substrate difficult. The increased risks of exposure to predation from small size alone would appear to be compensated by the combination of various morphological features. The same morphological features that act as camouflage in quiet pools likely may not serve the same function in riffle habitats (Page and Swofford 1984).

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